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Asynchronous food-web pathways could buffer the response of Serengeti predators to El Niño Southern Oscillation

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Abstract. Understanding how entire ecosystems maintain stability in the face of climatic and human disturbance is one of the most fundamental challenges in ecology. Theory suggests that a crucial factor determining the degree of ecosystem stability is simply the degree of synchrony with which different species in ecological food webs respond to environmental stochasticity. Ecosystems in which all food-web pathways are affected similarly by external disturbance should amplify variability in top carnivore abundance over time due to population interactions, whereas ecosystems in which a large fraction of pathways are nonresponsive or even inversely responsive to external disturbance will have more constant levels of abundance at upper trophic levels. To test the mechanism underlying this hypothesis, we used over half a century of demographic data for multiple species in the Serengeti (Tanzania) ecosystem to measure the degree of synchrony to variation imposed by an external environmental driver, the El Niño Southern Oscillation (ENSO). ENSO effects were mediated largely via changes in dry-season vs. wet-season rainfall and consequent changes in vegetation availability, propagating via bottom-up effects to higher levels of the Serengeti food web to influence herbivores, predators and parasites. Some species in the Serengeti food web responded to the influence of ENSO in opposite ways, whereas other species were insensitive to variation in ENSO. Although far from conclusive, our results suggest that a diffuse mixture of herbivore responses could help buffer top carnivores, such as Serengeti lions, from variability in climate. Future global climate changes that favor some pathways over others, however, could alter the effectiveness of such processes in the future.

Key words: demography; ecosystem stability; El Niño Southern Oscillation, ENSO; environmental stochasticity; rainfall; recruitment; Serengeti food web; Southern Oscillation Index, SOI; trophic interaction.

Introduction

Ecologists have long known that major disturbances such as elimination of top carnivores (Estes et al. 2011), weather (Coulson et al. 2001), epidemic disease outbreaks (Packer et al. 2005), or human hunting (Fryxell et al. 2010) can profoundly influence the abundance of wildlife populations. Given that all species are themselves embedded in complex food webs, often via nonlinear food-web interactions (May 1973, Murdoch et al. 2003, McCann 2012), it is reasonable to expect that such population perturbations will ripple outwards to affect other species in the food web (Ives et al. 2003, Ripa and Ives 2003, Ives and Carpenter 2007, McCann 2012). Surprisingly, however, the magnitude of ecosystem-wide responses to environmental perturbations has rarely been measured in a natural setting. This is an important gap in our understanding, particularly with the growing recognition that future changes in global climate are liable to include not only changes in expected levels of key environmental drivers such as temperature and precipitation, but increasing variability in those drivers.

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Here we present evidence that the El Niño Southern Oscillation (ENSO) contributes to fluctuations in several of the species in the Serengeti food web (see Plate 1). We show that the responses to changes caused by ENSO seemingly alternate, however, among different pathways in the Serengeti food web. Theory suggests that synchronized responses by multiple species should contribute to population perturbations via food-web interactions, leading to wide variation in abundance of all members of the food web (Ripa and Ives 2003). There is a richer range of possibilities, however, in systems in which there are inverse correlations in response, or lack of synchrony in response, to external environmental drivers for some species in the food web.

A simple mathematical model can be used to demonstrate the importance of these characteristics based on a simple food web composed of two herbivore prey species (of population densities X and Y, respectively) and a top carnivore of population density Z. Dynamics are described by the following stochastic version of a discrete-time Rosenzweig–MacArthur formulation:

$$X_{t+1} = X_t e^{a(1-X_t)-bZ_t+\varepsilon_t}$$

$$Y_{t+1} = Y_t e^{c(1-Y_t)-dZ_t+\gamma_t}$$

$$Z_{t+1} = Z_t e^{g(X_t+Y_t)-hZ_t}$$

where a, c, and g represent the maximum growth rates of prey 1, prey 2, and predators, respectively, b and d represent the prey attack rates by each predator, h represents the constant mortality rate of predators, and ε and γ represent environmental stochastic effects on prey 1 and prey 2, respectively. Note that prey densities are normalized such that each has an implicit carrying capacity = 1. We can use this simple model to consider three alternative scenarios. In the first scenario (Fig. 1a) both prey have correlated and identical demographic responses to a single climatic factor ($\gamma = \varepsilon$). This results in synchronized fluctuations in prey, with predators fluctuating considerably, slightly out of phase with their prey. In the second scenario (Fig. 1b) one herbivore species responds to environmental stochasticity, whereas the second herbivore species does not ($\gamma = 0$). This indifferent response by alternate prey to environmental stochasticity considerably dampens the amplitude of predator tracking of environmentally driven variation in the abundance of the primary prey species. Note that reduced variability in predator density is accompanied, however, by increased variability in prey density. In the third scenario (Fig. 1c) prey respond in an inversely correlated manner to climatic variability ($\gamma = -\varepsilon$). This results in out-of-phase fluctuations by different prey, resulting not surprisingly in even milder variability over time in predator abundance. This simple model suggests that out-of-phase or asynchronous effects on different food-web pathways could improve the long-term stability of top carnivores (Fig. 1d), illustrating an emergent food-web property that has previously gone unrecognized.

Materials and Methods

Monthly rainfall was recorded since 1937 from a gauge in the center of the Serengeti Ecosystem. Temperature data were obtained from the Climate Research Unit (CRU), University of East Anglia (Sinclair 1995, Brohan et al. 2006). The area of the ecosystem burned each dry season was recorded from the air at intervals since 1962 and recorded on maps, but since 2000 from satellite imagery using MODIS reflectance data (Rayner et al. 2003). Normalized difference vegetation index (NDVI) data prior to 2005 were downloaded from the Global Inventory Modeling and Mapping Studies (Tucker et al. 2004, 2005, Dempewolf et al. 2007) and for 2005–2009 were MODIS data downloaded from the Global Land Cover Facility (University of Maryland, College Park, Maryland, USA) (*available online*).[12] Ungulate age and sex classes were sampled twice yearly starting in 1962 for wildebeest (*Connochaetes taurinus*) and at various later times for other species fed upon by lions: topi (*Damaliscus lunatus*), zebra (*Equus burchelli*), kongoni (*Alcelaphus buselaphus*), waterbuck (*Kobus ellipsiprymnu*), and warthog (*Phacochoerus aethiopicus*). Rodent numbers were measured from twice-yearly live-trapping, and diurnal bird numbers were recorded from twice-yearly road transects since 1997. Earlier data were obtained from intermittent records back to 1968. Lion (*Panthera leo*) numbers, cub survival, and nutritional condition were recorded collected as part of long-term population studies (Packer et al. 2005). Anthrax cases were obtained from collected animal carcasses, and where possible cause of death has been recorded opportunistically by Park veterinarians since 1996 (Munson et al. 2008, Hampson et al. 2011).

Species that responded to rodent outbreaks were Black-shouldered Kite, Black-chested Snake-Eagle (*Circaetus pectoralis*), Brown Snake-Eagle (*C. cinereus*), Secretary Bird (*Sagittarius serpentarius*), and Black-headed Heron (*Ardea melanocephala*). Earlier Black-shouldered Kite outbreaks were recorded by A. R. E. Sinclair beginning in 1968. Long-term data sets for rodents (Senzota 1982, Packer 1983, Durant et al. 2007) and birds were calibrated by setting the highest value to 1 and calculating smaller values proportionally. Small-rodent-eating carnivores included black-backed jackal (*Canis mesomelas*), golden jackal (*Canis aureus*), side-striped jackal (*Canis adustus*), caracal (*Caracal caracal*), wildcat (*Felis silvestris*), serval (*Leptailurus serval*), common genet (*Genetta genetta*), honey badger (*Mellivora capensis*), and white-tailed mongoose (*Ichneumia albicauda*). These species were recorded from 1991 to 2006 (Durant et al. 2007) during daytime observations

[12] ftp://ftp.glcf.umd.edu/modis/500m/Africa/

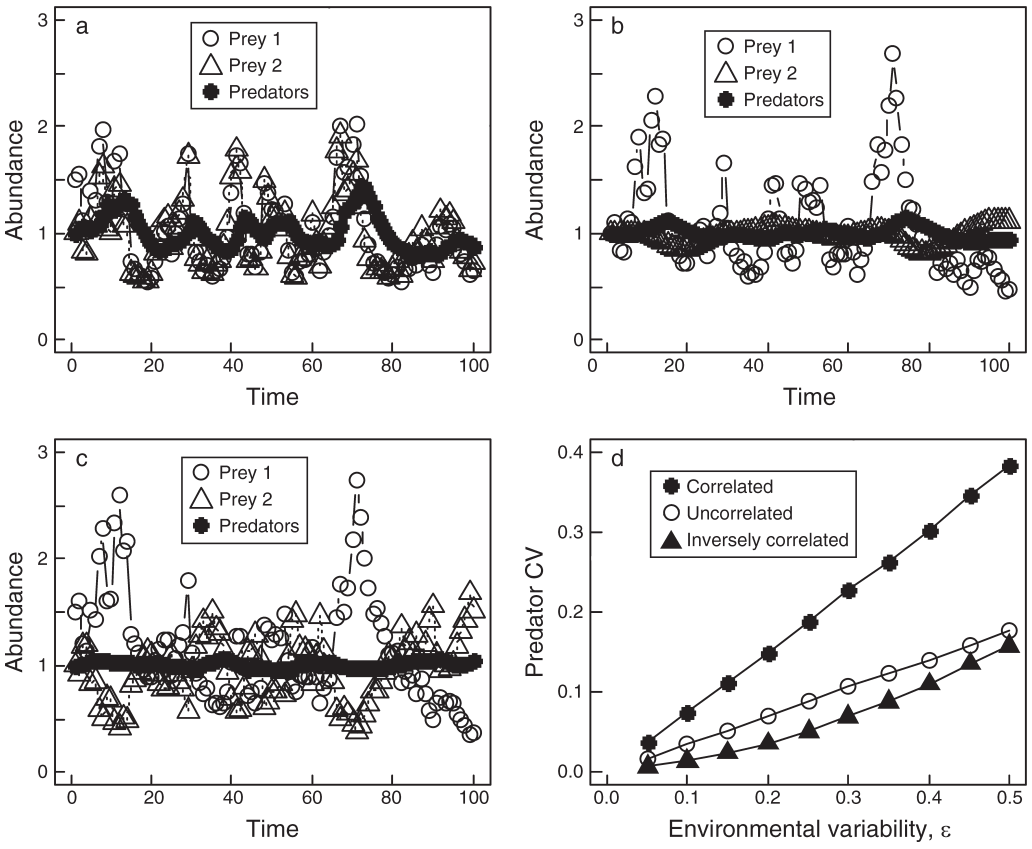

FIG. 1. Predicted changes over time for a model population of two herbivores and one predator that feeds indiscriminately on both prey species, with (a) correlated environmental stochasticity in growth rates of both prey, (b) inversely correlated environmental stochasticity among prey, and (c) alternate prey that are insensitive to environmental stochasticity affecting the first prey species. (d) Coefficient of variation (CV) in predator density as a function of the magnitude of environmental stochasticity (ε) in the scenarios in panels (a)–(c). Since this is a model there are no explicit units for time. Other parameter values for simulations were as follows: $a = 0.4$, $b = 0.4$, $c = 0.5$, $d = 0.4$, $g = 0.2$, and $h = 0.2$, where a, c, and g represent maximum growth rates of prey 1, prey 2, and predators, respectively; b and d represent prey attack rates by each predator; h represents the constant mortality rate of predators; and ε and γ represent environmental stochastic effects on prey 1 and prey 2, respectively. Note that prey densities are normalized such that each has an implicit carrying capacity = 1. We can use this simple model to consider three alternative scenarios. In the first scenario (Fig. 1a) both prey have correlated and identical demographic responses to a single climatic factor ($\gamma = \varepsilon$).

and since 2003 by the Carnivore Disease Project during monthly night transects using spotlights. Both sets were combined as above with 1 being the highest value.

All variables were tested for normality using the Shapiro–Wilk test. For variables that were not normally distributed we used the Spearman rank correlation, which makes no assumption about the distribution of the data. For all other variables, we tested the effects of climate using two approaches. First, we performed simple regressions between demographic variables and climatic drivers. Because such relationships can be confounded by autocorrelation effects and uncertain mixtures of process vs. observation error, we used multivariate autoregressive state-space (MARSS) models; Holmes et al. 2012) to evaluate the plausibility of alternate models that included Southern Oscillation Index (SOI), dry-season rainfall, wet-season rainfall, and predator density (in the case of large herbivores), or wildebeest yearling proportion (in the case of lions).

RESULTS

The Serengeti ecosystem is characterized by distinct dry and wet seasons. The wet season is further divided into two events, the "short rains" occurring in November to December and the "long rains" from March to June (Norton-Griffiths et al. 1975). These rainfall events are annually predictable, whereas the intensity and duration of rainfall within the wet and dry season is variable (Ritchie 2008). The ENSO as measured by the Southern Oscillation Index (SOI) drives the dynamics of the Serengeti ecosystem through its influence on rainfall, temperature, and vegetation abundance. Here we demonstrate the existence of two different food-web pathways that are influenced through SOI effects on

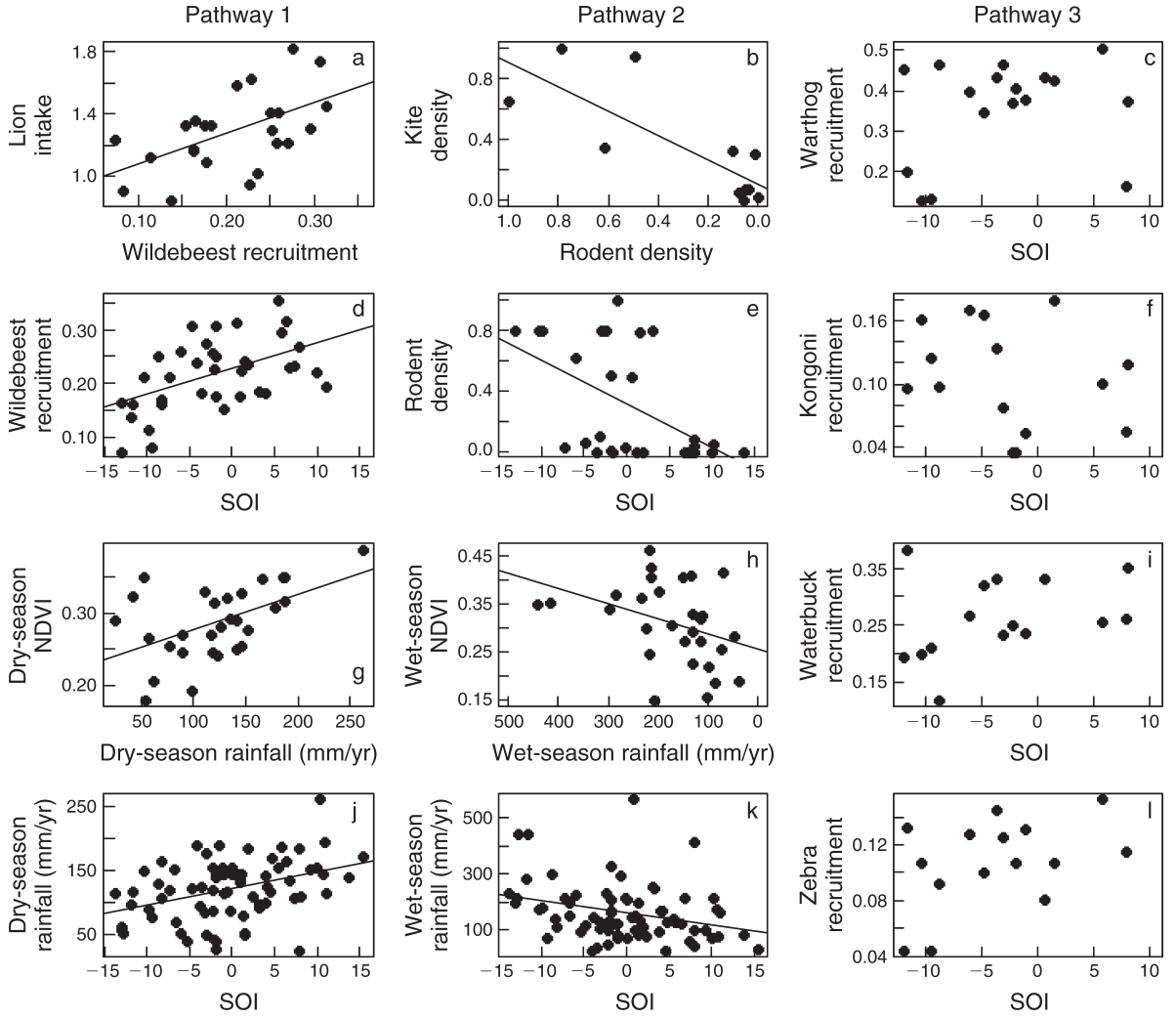

FIG. 2. Pathway 1 (left-hand column): the Southern Oscillation Index (SOI) is positively related to (j) the amount of rain falling in the subsequent dry season (July–October), and that in turn is related to (g) vegetation abundance (based on normalized difference vegetation index) during the dry season. Extreme positive values of SOI increase (d) the proportion of yearlings recruited to the wildebeest population, which in turn positively stimulates feeding rates of (a) lions. Pathway 2 (center column): the SOI is negatively related to (k) the amount of rain falling in the subsequent short rains in November–December, which affects (h) vegetation abundance during the wet season. As a result (e) rodent populations are depressed in years with peak values of the SOI. (b) Populations of Black-shouldered Kites closely follow the abundance of rodents with a 1-yr time lag. Pathway 3 (right-hand column): there is no statistically significant effect of SOI on recruitment of (c) warthog, (f) kongoni, (i) waterbuck, or (l) zebra. Lion intake is an index, 0–2; kite density is an index, 0–1; rodent density is an index, 0–1. Herbivore recruitment rates are reported in units of yearlings/female adult.

rainfall in the dry season or effects on rainfall during the short rains (hereafter termed "wet- season effects"). We first consider the effects of SOI on dry-season rainfall.

SOI was positively related to rainfall in the dry-season months of July–October as measured from monthly rainfall records in the center of Serengeti since 1937 ($R^2 = 0.14$, $n = 73$ yr, $P = 0.001$) (Fig. 2j). The monthly average daily maximum temperature during the dry season in the Serengeti has been negatively related to SOI since 1937 ($R^2 = 0.09$, $n = 73$ yr, $P = 0.01$). The relationship of SOI with dry season rainfall was further improved with the addition of temperature ($R^2 = 0.19$, $P < 0.001$) such that higher SOI was associated with more rainfall and cooler temperatures. Primary productivity during the dry season can be estimated from the NDVI collected by satellite data from 1981 to 2009. Dry season NDVI was positively correlated with SOI ($R^2 = 0.35$, $n = 28$ yr, $P < 0.001$) because primary productivity during the dry season was determined by dry season rainfall ($R^2 = 0.27$, $P < 0.004$) (Fig. 2g).

The migratory population of 1.5 million wildebeest (*Connochaetes taurinus*) is a keystone species (Sinclair et al. 1985, 2007, 2010, Mduma et al. 1999, Holdo et al. 2009*a*, *b*), influencing multiple other species in the

PLATE 1. Topi mother feeding her offspring in Serengeti National Park. Recruitment of topi yearlings is positively influenced by ENSO variability, through links in dry season rainfall and food availability. Photo credit: J. M. Fryxell.

Serengeti food web. The wildebeest migration tracks changes in food availability triggered by local rainfall patterns (Holdo et al. 2009*a*). During the dry season, wildebeest herds migrate north to areas that receive greater rainfall during these dry months. During the wet season, the herds travel south to the short-grass plains. Wildebeest have a highly synchronized calving event that coincides with the wet-season rainfall on the short-grass plains (Holdo et al. 2009*a*). The movements and population dynamics of the migrants then affect other components of the ecosystem (Holdo et al. 2009*a*, *b*; Mduma et al. 1999, Sinclair et al. 1985, 2007, 2010).

The proportion of wildebeest yearlings (aged 13–24 months) in the population, which has pivotal influence on the population rate of increase in ungulates, was positively correlated with the mean annual SOI over their first year of life (Fig. 2d) ($R^2 = 0.37$, $n = 37$ yr, $P < 0.001$). Multivariate autoregression state-space (MARSS) models suggested that variation in both SOI and adult lion density had demonstrable effects on variation in wildebeest recruitment (ΔAIC < 1 for all models including SOI, lion density, or both compared to ΔAIC > 2 for models that also included dry season rainfall as a covariate). A closely related antelope, topi (*Damaliscus lunatus*), also showed a positive relationship between yearling proportion and SOI ($R^2 = 0.27$, $n = 33$ yr, $P < 0.01$). MARSS models suggested that variation in lion density, SOI or dry season rainfall acting in isolation or SOI + dry season rainfall were all plausible (ΔAIC ≤ 1) in explaining variation in topi recruitment compared to other combinations of these variables (ΔAIC >2).

SOI presumably influenced wildebeest and topi population growth via rainfall and grass growth occurring during the dry season (Fig. 2g), with an additional influence of temperature. Dry-season grass production determines wildebeest calf survival (Mduma et al. 1999) because food availability is most limiting at this time of year, resulting in positive relationships between yearling recruitment and SOI. In contrast, higher dry-season temperatures, associated with less rain, desiccate grass regrowth, restrict grazing, and limit food intake in Serengeti ungulates, and thus exacerbate the effect of low rainfall.

Higher up the food chain there is some suggestion that residual cub recruitment in the Serengeti lion (*Panthera leo*), after controlling for male takeover frequency, was

positively linked to variability in SOI ($R^2 = 0.09$, $n = 42$ yr, $P = 0.046$). Lion population dynamics have been linked to changes in wildebeest numbers over the past 40 years (Packer et al. 2005), which themselves are related to higher rainfall. MARSS models suggested that SOI, dry-season rainfall, and wildebeest recruitment were all equally plausible as covariates influencing residual lion cub recruitment (ΔAIC < 0.5 for all models including SOI, dry-season rainfall, or wildebeest recruitment compared to ΔAIC > 1.8 for more complex models that included combinations of these variables). Lion belly size, which is used as an index of feeding success, was greater in years with higher proportions of yearling wildebeest ($R^2 = 0.28$, $n = 29$ yr, $P = 0.01$; Fig. 2a). Prey capture success by lions seemingly affects cub recruitment, which increases with dry-season rainfall in woodland lions (Mosser et al. 2009), after controlling for the effect of pride takeovers by male lions (combined model $R^2 = 0.17$, $P = 0.009$), because incoming males routinely eliminate the dependent offspring of prior coalitions (Packer et al. 2001).

Disease outbreaks in ungulates were also linked to SOI. Grazer deaths from anthrax in the dry season are positively correlated with SOI (Poisson regression, $P < 0.0001$, $n = 14$ yr , Poisson regression coefficient $= 0.14$) (Hampson et al. 2011). Both prolonged drought and heavy rains are implicated in disease outbreaks (Munson et al. 2008, Hampson et al. 2011) and these events are partially defined by SOI patterns. In other words, climate variation caused by ENSO events triggers synchronized responses of dry season food availability, large herbivores, lions, and parasites along a major pathway of the Serengeti food web (Fig. 2).

We have identified a second food-web pathway in Serengeti that is influenced by SOI, but with an inverse pattern to that shown by dry-season NDVI, wildebeest, and lions. This second pathway is mediated via rainfall occurring during the wet season, which is negatively related to SOI ($R^2 = 0.18$, $n = 73$ yr, $P < 0.001$; Fig. 2k). Monitoring of rodent numbers in the Serengeti woodlands from 1968 to 2009 has revealed eruptions every 5–6 years, consistent with the periodic fluctuations well documented in agricultural regions elsewhere in Tanzania (Leirs et al. 1996, 1997). Rodent abundance in Serengeti was negatively related to SOI over the 38-year period ($r_S = -0.49$, $n = 28$ yr, $P = 0.008$) (Fig. 2e), probably because of the link between SOI and wet season vegetation abundance (Fig. 2h). Rodent outbreaks occurred during years of high rainfall during November–December ($R^2 = 0.34$, $n = 19$ yr, $P = 0.002$), as seen elsewhere in Tanzania (Leirs et al. 1996, 1997), explaining the negative relationship of rodent outbreaks to SOI. While variation in SOI offered the most parsimonious explanation for the observed changes in rodent abundance, MARSS models suggested that wet-season rainfall, dry-season rainfall, and combinations of variables were also plausible as covariates (ΔAIC < 2).

Climate variation in SOI synchronizes the population responses of rodents and their predator populations. Numbers of the black-shouldered kite (*Elanus caeruleus*), a rodent specialist, increased one year after a rodent eruption ($R^2 = 0.64$, $P < 0.001$) (Fig. 2b). It was not possible to test the effect of rodent density using MARSS, because the algorithm cannot handle missing values for covariates. The abundance of seven species of small carnivores since 1991 was correlated (albeit with marginal significance) with rodent abundance the previous year ($R^2 = 0.21$, $n = 19$ yr, $P = 0.07$). Four other diurnal, rodent-eating birds showed similar responses. In other words, the Serengeti food web has a second major pathway triggered by wet-season augmentation of food resources, affecting rodent populations and their predator species (Fig. 2). Interestingly, this second pathway fluctuates out of phase with the dry-season rainfall–NDVI–wildebeest–lion–anthrax pathway.

Finally, regression tests for several other species of large herbivore eaten by lions showed no statistically significant relationships ($P > 0.10$) between recruitment and SOI (Fig. 2c, f, i, l): zebra, kongoni, waterbuck, and warthog. These species represent yet a third pathway in the Serengeti food web, one that was unresponsive to climatic variation in SOI. The unresponsive species of ungulates give birth throughout the year (Sinclair et al. 2000), which may buffer them from the seasonal effects of SOI because poorer conditions in one season are compensated by better conditions at other times of year. This may represent an adaptive strategy to counter the effects of prolonged drought (Martyn Murray, *personal communication*). In contrast, wildebeest and topi have highly synchronized birth periods—wildebeest in February–March, topi in October–November—that may make them more sensitive to environmental variation.

Discussion

Previous studies have shown that variation in ENSO influences primary productivity in semiarid systems of Australia (Holmgren et al. 2006), small-mammal populations in South America (Lima et al. 2002), and rainfall in southern (Ogutu and Owen-Smith 2003) and eastern Africa. ENSO also explains differences in ecosystem productivity (Ogutu et al. 2008, Oba et al. 2001, Anyamba et al. 2002) and the consequent effects of ENSO on rainfall contributed significantly to variation in demographic patterns for several ungulate species, but interestingly not wildebeest (Owen-Smith et al. 2005, Owen-Smith and Mills 2006, 2008) in South Africa. ENSO events also have noteworthy effects in Serengeti, but with an important twist: different pathways of the Serengeti food web have contrasting responses to the same environmental driver. Some herbivores prosper in years with positive SOI (e.g., wildebeest and topi), whereas other species suffer (e.g., rodents). At the same time a third group of species is

unaffected by ENSO (e.g., year-round-breeding ungulates such as zebra).

Stochastic food-web theory is in its infancy (Ives et al. 2003, Ripa and Ives 2003, McCann and Rooney 2009), so we can only speculate in crude terms about the potential significance of the observed demographic responses to climate variation. The simple model we outlined at the outset suggests that asynchronous effects of ENSO on different food-web pathways could potentially buffer variation in Serengeti carnivore populations that would otherwise be expected (Fig. 1d), although a truly rigorous test would require comparisons across multiple ecosystems with differing responses to environmental stochasticity. Neutral responses to ENSO variation by some herbivores in the food web is no doubt more important in buffering predator variability than out-of-phase variation by small mammals, simply because few carnivores in Serengeti feed on both small mammals and ungulates. Note that even though asynchronous dynamics may help to stabilize top carnivore populations, our simple models suggest that this effect would likely come at the cost of increased variability on prey abundance. Similarly complex linkages among weather, demography, and predator–prey interactions are suggested by time-series data from Kruger National Park (Owen-Smith et al. 2005, Owen-Smith and Mills 2006, 2008).

Should future global alteration in climate alter the strength, direction, or frequency of ENSO events, however, the situation could change. This could impact the stability of the Serengeti ecosystem by favoring one food-web pathway over others or by amplifying environmental stochasticity. For example, there has been a gradual increase in dry-season rainfall in Serengeti over the past half century, whereas wet-season rainfall has slowly declined (Ritchie 2008). If we assume that such trends persist into the future, one might predict that this would be favorable to wildebeest, topi, and lions, but detrimental to rodents and black-shouldered kites, as well as a suite of other small carnivores. On the other hand, we might expect future changes in a suite of related physical (temperature, evapotranspiration, CO_2) and biotic (diversity, balance between woody plants and graminoids) processes that could be of even greater importance (Ritchie 2008). In any case, we conjecture that any future climate change that alters the degree of food-web synchrony itself could increase variability in top carnivores, irrespective of the changes in magnitude of climatic environmental drivers. Given that top carnivores often have low population densities, such changes could accordingly have serious conservation implications.

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Literature Cited

Anyamba, A., C. J. Tucker, and R. Mahoney. 2002. From El Niño to La Niña: vegetation response patterns over East and Southern Africa during the 1997–2000 period. Journal of Climate 15:3096–3103.

Brohan, P., J. J. Kennedy, I. Harris, S. F. B. Tett, and P. D. Jones. 2006. Uncertainty estimates in regional and global observed temperature changes: a new data set from 1850. Journal of Geophysical Research 111(D12):D12106.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Dempewolf, J., S. Trigg, R. S. DeFries, and S. Eby. 2007. Burned-area mapping of the Serengeti–Mara region using MODIS reflectance data. IEEE Geoscience and Remote Sensing Letters 4:312–316.

Durant, S. M., S. Bashir, T. Maddox, and M. K. Laurenson. 2007. Relating long-term studies to conservation practice: the case of the Serengeti Cheetah Project. Conservation Biology 21:602–611.

Estes, J. A., et al. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

Fryxell, J. M., C. Packer, K. S. McCann, E. J. Solberg, and B. E. Saether. 2010. Resource management cycles and the sustainability of harvested wildlife populations. Science 328: 903–906.

Hampson, K., et al. T. 2011. Predictability of anthrax infection in the Serengeti, Tanzania. Journal of Applied Ecology 48(6): 1333–1344.

Holdo, R. M., R. D. Holt, and J. M. Fryxell. 2009*a*. Opposing rainfall and plant nutritional gradients best explain the wildebeest migration in the Serengeti. American Naturalist 173:431–445.

Holdo, R. M., A. R. E. Sinclair, K. L. Metzger, B. M. Bolker, A. P. Dobson, M. E. Ritchie, and R. D. Holt. 2009*b*. A disease-mediated trophic cascade in the Serengeti and its implications for ecosystem C. PLoS Biology 7(9):e1000210.

Holmes, E. E., E. J. Ward, and K. Wills. 2012. Marss: multivariate autoregressive state-space models for analyzing time-series data. The R Journal 4:11–19.

Holmgren, M., et al. 2006. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environment 4:87–95.

Ives, A. R., and S. L. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Ives, A. R., B. Dennis, K. L. Cottingham, and S. L. Carpenter. 2003. Estimating community stability and ecological interactions from time-series data. Ecological Monographs 73: 301–330.

Leirs, H., N. C. Stenseth, J. D. Nichols, J. E. Hines, R. Verhagen, and W. Verheyen. 1997. Stochastic seasonality and nonlinear density-dependent factors regulate population size in an African rodent. Nature 389:176–180.

Leirs, H., R. Verhagen, W. Verheyen, P. Mwanjabe, and T. Mbise. 1996. Forecasting rodent outbreaks in Africa: an ecological basis for *Mastomys* control in Tanzania. Journal of Applied Ecology 33:937–943.

Lima, M., N. C. Stenseth, and F. M. Jaksic. 2002. Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecology Letters 5:273–284.

May, R. M. 1973. Diversity and stability in model ecosystems. Princeton University Press, Princeton, New Jersey, USA.

McCann, K. S. 2012. Food webs. Princeton University Press, Princeton, New Jersey, USA.
McCann, K. S., and N. Rooney. 2009. The more food webs change, the more they stay the same. Philosophical Transactions of the Royal Society B 364:1789–1801.
Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology 68:1101–1122.
Mosser, A., J. M. Fryxell, L. Eberly, and C. Packer. 2009. Serengeti real estate: density versus fitness-based indicators of lion habitat quality. Ecology Letters 12:1050–1060.
Munson, L., K. A. Terio, R. Kock, T. Mlengeya, M. E. Roelke, D. Dubovi, B. Summers, A. R. E. Sinclair, and C. Packer. 2008. Climate extremes promote fatal co-infections during canine distemper epidemics in African lions. PLoS ONE 3(6): e2545.
Murdoch, W. W., C. J. Briggs, and R. M. Nisbet. 2003. *Consumer-resource dynamics*. Princeton University Press, Princeton, New Jersey, USA.
Norton-Griffiths, M., D. Herlocker, and L. Pennycuick. 1975. The patterns of rainfall in the Serengeti ecosystem, Tanzania. East African Wildlife Journal 13:347–374.
Oba, G., E. Post, and N. C. Stenseth. 2001. Sub-saharan desertification and productivity are linked to hemispheric climate variability. Global Change Biology 7:241–246.
Ogutu, J. O., and N. Owen-Smith. 2003. ENSO, rainfall and temperature influences on extreme population declines among African savanna ungulates. Ecology Letters 6:412–419.
Ogutu, J. O., H. P. Piepho, H. T. Dublin, N. Bhola, and R. S. Reid. 2008. El Niño-Southern Oscillation, rainfall, temperature and Normalized Difference Vegetation Index fluctuations in the Mara-Serengeti ecosystem. African Journal of Ecology 46:132–143.
Owen-Smith, N., D. R. Mason, and J. O. Ogutu. 2005. Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. Journal of Animal Ecology 74:774–788.
Owen-Smith, N., and M. G. L. Mills. 2006. Manifold interaction influences on the population dynamics of a multi-species ungulate assemblage. Ecological Monographs 76:73–92.
Owen-Smith, N., and M. G. L. Mills. 2008. Shifting prey selection generates contrasting herbivore dynamics within a large-mammal predator-prey web. Ecology 89:1120–1133.
Packer, C. 1983. Demographic changes in a colony of Nile grassrats (*Arvicanthis niloticus*) in Tanzania. Journal of Mammalogy 64:159–161.
Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territory, and population dynamics in Serengeti lions. Science 307:390–393.
Packer, C., A. E. Pusey, and L. E. Eberly. 2001. Egalitarianism in female African lions. Science 293:690–693.
Rayner, N. A., D. E. Parker, E. B. Horton, C. K. Folland, L. V. Alexander, D. P. Rowell, E. C. Kent, and A. Kaplan. 2003. Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. Journal of Geophysical Research 108(D14):4407.
Ripa, J., and A. R. Ives. 2003. Food web dynamics in correlated and autocorrelated environments. Theoretical Population Biology 64:369–384.
Ritchie, M. 2008. Global environmental changes and their impact on the Serengeti. Pages 138–208 *in* A. R. E. Sinclair, C. Packer, S. A. R. Mduma, and J. M. Fryxell, editors. Serengeti III: human impacts on ecosystem dynamics, University of Chicago Press, Chicago, Illinois, USA.
Senzota, R. B. M. 1982. The habitat and food habits of the grass rats (*Arvicanthis niloticus*) in the Serengeti National Park, Tanzania. African Journal of Ecology 20:241–252.
Sinclair, A. R. E. 1995. Population limitation of resident herbivores. Pages 3–10 *in* A. R. E. Sinclair and P. Arcese, editors. Serengeti II: dynamics, management and conservation of an ecosystem. University of Chicago Press, Chicago, Illinois, USA.
Sinclair, A. R. E., H. Dublin, and M. Borner. 1985. Population regulation of Serengeti wildebeest: a test of the food hypothesis. Oecologia 65:266–268.
Sinclair, A. R. E., S. A. R. Mduma, and P. Arcese. 2000. What determines phenology and synchrony of ungulate breeding in Serengeti? Ecology 81:2100–2111.
Sinclair, A. R. E., S. A. R. Mduma, J. G. C. Hopcraft, J. M. Fryxell, R. Hilborn, and S. Thirgood. 2007. Long-term ecosystem dynamics in the Serengeti: lessons for conservation. Conservation Biology 21:580–590.
Sinclair, A. R. E., K. Metzger, J. S. Brashares, A. Nkwabi, G. Sharam, and J. M. Fryxell. 2010. Trophic cascades in African savannas: Serengeti as a case study. Pages 255–274 *in* J. Terborgh and J. A. Estes, editors. Trophic cascades: predators, prey and the changing dynamics of nature, Island Press, Washington, D.C., USA.
Tucker, C. J., J. Pinzon, and M. E. Brown. 2004. Global inventory modeling and mapping studies. NA94apr15b.n11-Vlg, 2.0. Global Land Cover Facility, University of Maryland, College Park, Maryland, USA.
Tucker, C. J., J. E. Pinzon, M. E. Brown, D. A. Slayback, E. W. Pak, R. Mahoney, E. F. Vermote, and N. El Saleous. 2005. An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. International Journal of Remote Sensing 26:4485–4498.

Supplemental Material

Supplement

R code for computer simulation model of time dynamics of predator and two prey species shown in Fig. 1 (*Ecological Archives* E094-100-S1).